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Preliminary Review of the Specimens and Localities of Platyrrhine Fossils from the Tatacoa Desert, Colombia

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INTRODUCTION

Since the first primate fossils were collected in 1940s (Stirton, 1951), many platyrrhine fossils have been recovered from the middle Miocene La Venta deposits. The recovery of those primate fossils have revealed the features of the La Venta primate fauna and contributed for understanding the evolutionary process of platyrrhine monkeys. As well known, all La Venta primate taxa are easily related to the extant platyrrhines, suggesting that most living platyrrhine lineage have appeared at least by the middle Miocene age. In contrast, other Neogene fossil primates recovered in Bolivia (latest Oligocene), Chile (early Miocene), and Patagonia (early to middle Miocene) are rather hard to allocate to the extant taxa. Such phenetic differences between the "modern" La Venta platyrrhine fauna and the "archaic" platyrrhine fauna of other localities may be expalined by two different interpretations: (1) The "modern" La Venta platyrrhine fauna is a result of the dispersion of early platyrrhines, which had invaded from Africa through southern South American continent. In this hypothesis all the extant platyrrhine taxa have originated from "Laventan primates". (2) The "modern" La Venta platyrrhine fauna is a regional evolutionary radiation of middle Miocene platyrrhines, which had already evolved from the "archaic" platyrrhine grade.

The further excavation of primate fossils in La Venta badlands will lead an answer to this question. In this paper, in order to make clear the feature of the La Venta platyrrhine fauna, we list all the primate fossil specimens, which have been recovered to date, concerning their locality and horizon.

The following abbrebiations are used in this paper: INGEOMINAS, Instituto de Investigaciones en Geociencias, Mineria y Quimica; UCMP, University of California, Museum of Paleontology; KU, Kyoto University; DU, Duke University.

PRIMATE TAXA FROM LA VENTA BADLANDS

The primate taxa recovered in La Venta are listed in Table 1-4. In 1940s University of California Expeditions have recovered the first primate fossils: the holotypes of *Stirtonia tatacoensis*, *Cebupithecia sarmientoi*, and *Neosaimiri fieldsi* (Stirton, 1951). In 1977 Kyoto University (Japan)

and INGEOMINAS (Colombia) joint expedition teams started the paleontòlogical excavations in the Tatacoa Desert and recovered many fossil specimens: dozens of isolated teeth of *S. tatacoensis* (Setoguchi *et al.*, 1981), *Kondous laventicus* (Setoguchi, 1985), *Micodon kiotensis* (Setoguchi and Rosenberger, 1985), *Aotus dindensis* (Setoguchi and Rosenberger, 1987), a new specimen of *C. sarmientoi* (Setoguchi *et al.*, 1988), *Laventiana annectens* (Rosenberger *et al.*, 1991), numerous isolated teeth and postcranial remains of *N. fieldsi* (Takai, 1994; Nakatsukasa *et al.*, in prep.), several postcranial remains referred to *A. dindensis* and *Neosaimiri* (Gebo *et al.*, 1990), and a new specimen of *S. victoriae* (Takai *et al.*, in prep).

Since 1980 Duke University-INGEOMINAS joint teams have also carried out the investigations and recovered many primate fossils in the Tatacoa Desert: *Mohanamico hershkovitzi* (Luchterhand *et al.*, 1986), *Stirtonia victoriae* (Kay *et al.*, 1987), several postcranial remains of *C. sarmientoi* and of another unknown species (Meldrum, 1990; Meldrum *et al.*, 1990; Meldrum, 1993; Meldrum and Kay, in press; Ford et al., 1991), *Lagonimico conclucatus* (Kay, 1994), a new callitrichine (Kay and Meldrum, in press), and a new pitheciine (Kay, personal comunication).

Some of those fossil taxa are controversial for their validity as an independent taxon. For instance, Setoguchi (1985) described a new genus and species, "*Kondous laventicus*," on the basis of two isolated upper molars, which were discovered together with dozens of isolated teeth of *S. tatacoensis*, and regarded it as a probable ancestor of extant spider monkeys, *Ateles*. Later, however, Kay *et al.* (1987) demonstrated that they are isolated M^3s of *S. tatacoensis* by copmaparing them with another species of*Stirtonia*.

As another example, "*Laventiana annectens*", the type of which is a nearly complete mandible with right and left C_1-M_2, was originally described as a new genus and species (Rosenberger *et al.*, 1991), but Takai (1994) proved "*Laventiana*" to be a junior synonym of *Neosaimiri* by examining numerous isolated teeth collected from the same locality as "*Laventiana*".

Mohanamico hershkovitzi and *Aotus dindensis* were recovered at El Dinde in 1980 by Duke University team and in 1986 by Kyoto University team, respectively (Luchterhand et al., 1986; Rosenberger and Setoguchi, 1987). Now several researchers regard *A. dindensis* and *M. hershkovitzi* as a single taxon related to the extant pitheciines (e. g. Kay, 1990), whereas others insist that they are different taxa related to extant *Aotus* and *Callimico* respectively (e. g. Rosenberger *et al.*, 1990). In this case, not only the taxonomic identification but also the allocation even to the subfamily level remains debatable.

These taxonomic problem is caused partly by the obscurity ans confusion among the location and horizon where fossil specimens were recovered.

GEOLOGY AND STRATIGRAPHY OF THE LA VENTA SEDIMENTS

The fluvial deposits exposed in the Tatacoa desert (= La Venta badlands) are considered the upper part of the Honda Group (Fields, 1959; Van Houten and Travis, 1968; Wellman, 1970). Wellman (1970) divided "La Venta sediments" into two formations: the La Dorada Formation (lower), composed of the Puerto Salgar and Perico Members, and the Villavieja Formation (upper), composed of the Baraya Volcanic and Cerro Colorado Redbed Members. He established a general geology of

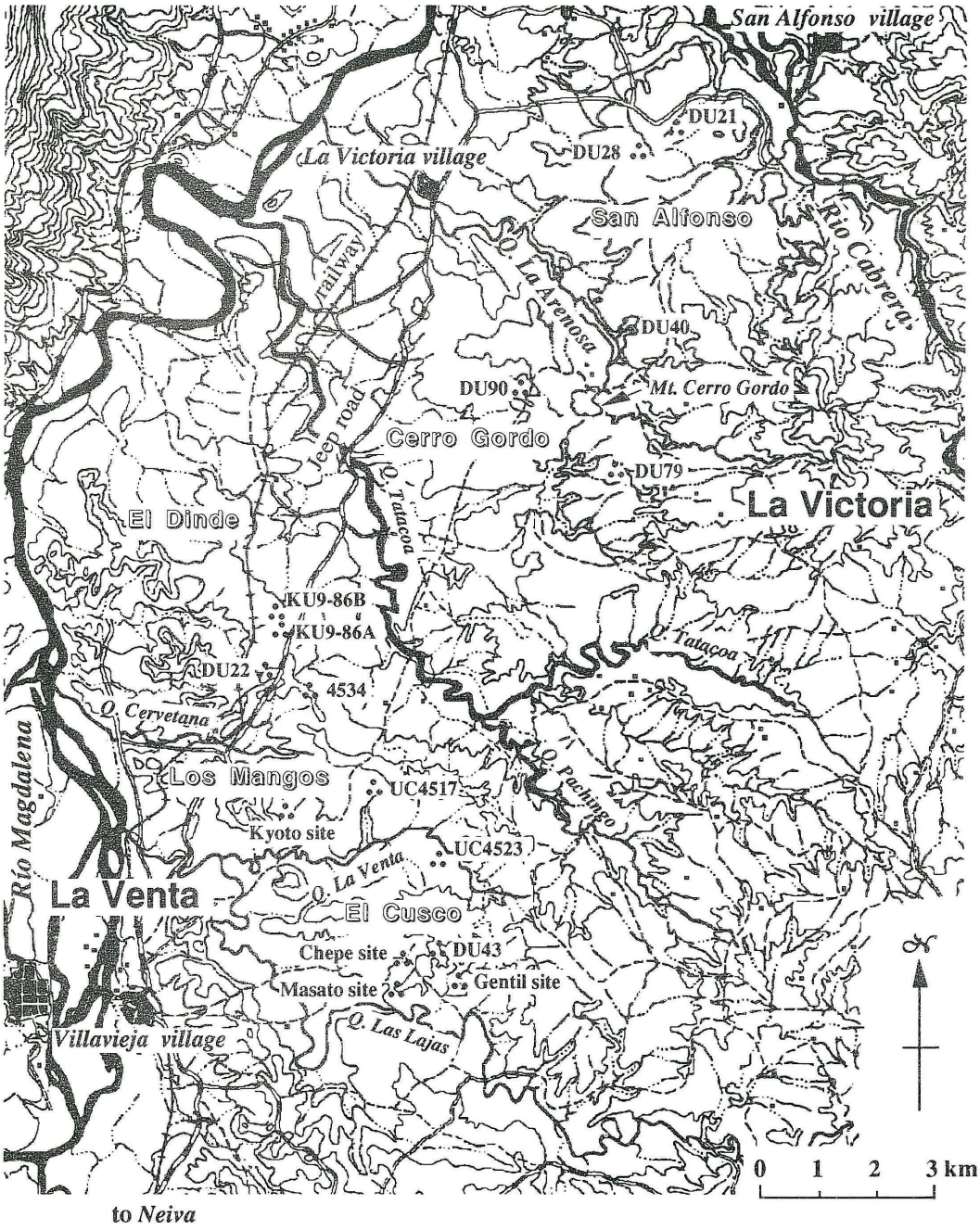

Figure 1. Locality Map of the Tatacoa Desert. ∴ means primate fossil localities. UC: University of California; KU: Kyoto University; DU: Duke university.

Upper Magdalena Valley, Colombia, but it is too general to adopt for the detailed local geology of the present survey area.

The detailed stratigraphy of "La Venta sediments" has been studied by several workers. Fields (1959) established a framework of the geology of "La Venta" for the first time, and regarded the La Venta fauna as the late Miocene, Friasian Land Mammal Age. His framework is basically accepted by many workers except several points at issue: the geologic age of the La Venta sediments is now considered as the Middle Miocene (e.g. MacKenna, 1980), and Kay *et al.* (1987) insist that the La Venta fauna is more similar to Santacrucian than Friasian assemblages. Madden *et al.* (in press) propose a new South American Land Mammal Age, the Laventan, for the La Venta mammalian fauna. Moreover, the thickness of the sediments and the minor structure of the survey area were corrected by several workers (e.g. Takai *et al.*, 1992; Guerrero, in press).

Takai *et al.* (1992) established the Villavieja Formation of Wellman (1970), dividing it into four distinct members (Molina, Los Mangos Red, Las Lajas, and Tatacoa Red Members). They united several informal units of Fields (1959), such as "Fish Bed" or "Monkey Unit", into a new stratigraphic unit, Molina Member. In addition, they calculated the thickness of the Villavieja Formation as 133 to 154 meters, which is about half of the Fields' estimation (262.5 meters thick; Fields. 1959).

Guerrero (in press) also provides a stratigraphic framework of the "La Venta beds", dividing them into two formations, La Victoria Formation (lower) and Villavieja Formation (upper). In his framework (Guerrero, in press) the "Villavieja Formation" means much thicker strata, including the "San Francisco Sandstone Beds" and "Polonia Red Beds", whereas the Villavieja Formation of Takai *et al.* (1992) corresponds to the "Baraya Member" and the "El Cordón Red Beds" of Guerrero (in press). Thus, the stratigraphic nomenclature is not standerized. In this paper we adopt the Villavieja Formation, defined by Takai *et al.* (1992) and the La Victoria Formation defined by Guerrero (in press) because of their detailed geological work at each strata (Fig. 2).

The radioisotopic ages were also obtained recently by several workers. Takemura and Danhara (1985) reported the fission-track dates (15.7±1.1, 14.6±1.1 and 16.1±0.9 Ma) from the Molina Member and Los Mangos Red Member, suggesting the middle Miocene age. Takemura *et al.* (1992) also calculated the fission-track dates (13.6±0.5, 13.6±0.7 and 12.6±0.5 Ma) from the lower part of the Tatacoa Red Member, 50-100 meters higher than the fission-track sampling horizons of Takemura and Danhara (1985). Guerrero (in press) reported some radioisotopic ages and estimated that the La Victoria (lower) and Villavieja Formations were deposited from 13.5 to 12.9 Ma, and 12.9 to 11.5 Ma respectively. Therefore, the current available data coincidentally indicate that the La Venta sediments, especially the Villavieja Formation, were deposited during the Middle Miocene age, more or less 12 to 13 Ma.

PRIMATE FOSSIL LOCALITIES

A detailed map of La Venta badlands is shown in figure 1. All the locations of primate fossils are usually described by the locality number, such as Kyoto locality 9-86A, which does not make sense for other workers. Moreover, the local place-names in La Venta are rather confused now. For

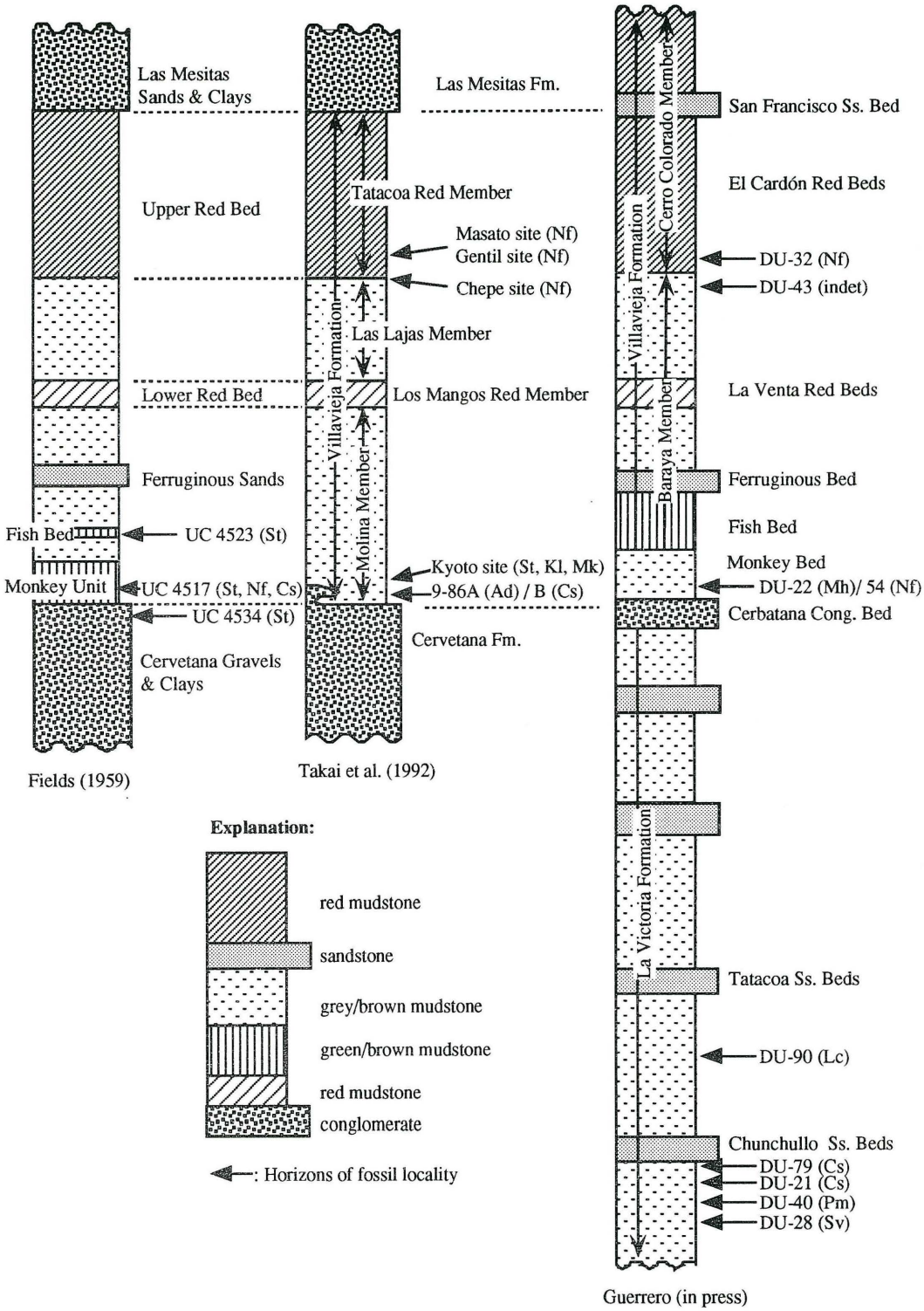

Figure 2. Schematic stratigraphic sections of the Honda Group in the Tatacoa Desert, showing the horizons of fossil localities. UC: University of California; KU: Kyoto University; DU: Duke University. Taxonomic name is shown in parenthesis: St = *S. tatacoensis*; Sv = *S. victoriae*; Kl = *Kondous*; Mk = *Micodon*; Mh = *Mohanamico*; Ad = *A. dindensis*; Cs = *Cebupithecia*; Nf = *Neosaimiri*; Lc = *Lagonimico*; Pm = new callitrichine form.

example, "La Venta" is very famous place-name for paleoprimatologists as a middle Miocene platyrrhine fossil locality, but "La Venta" originally indicates a very small area between two rivers, Quebrada Cervetana and Q. La Venta, where the type specimens of *Cebupithecia* and *Neosaimiri* were collected (Stirton, 1951). Local people call the "La Venta badlands" as the Tatacoa Desert (= Desierto de la Tatacoa in Spanish), though the former is much more famous for us.

Though the locality number should be described first, an appropriate local subdivision is also necessary to clear up the distribution of the fossil localities. So, in this paper we propose a local division of the survey area: La Victoria (northern part) and La Venta (southern part) regions, separated by Quebrada Tatacoa, and both regions are subdivided into several areas. Of course this subdivision is just for convenience, and does not always correspond to the stratigraphic division. Avoiding an unnecessary confusion, we would like to call the survey area the Tatacoa Desert in this paper.

La Victoria region

La Victoria region is a northern side of Quebrada Tatacoa, and is divided into two areas, San Alfonso and Cerro Gordo by Quebrada Arenosa (Fig. 1). La Victoria village is situated at the right bank of Q. Arenosa, and about 15 km NNE of Villavieja village. San Alfonso village is located at the right bank of Río Cabrera, and there is a jeep road between Villavieja and San Alfonso via La Victoria. The sediments of La Victoria region roughly correspond to the La Victoria Formation of Guerrero (in press).

San Alfonso: At San Alfonso a large-size fossil platyrrhine, *Stirtonia victoriae*, has been discovered (Kay *et al.*, 1987). This second species of *Stirtonia* is moderately larger than the type species, *S. tatacoensis*, and have a well-developed stylar shelf/cusps and have the three-rooted P^{3-4}. The type locality of *S. victoriae* is Duke locality 28, about 4.25 km WSW of San Alfonso village (Kay *et al.*, 1987; see Fig. 1). At the same location another specimens, isolated P_2 and P_3, were recovered by Kyoto University team in 1994 (Takai *et al.*, in prep.). These new specimens are referable to *S. victoriae* because of their large-size.

Kay *et al.* (1987) estimate that the horizon of the Duke locality 28 is approximately 290 meters below the type locality of *S. tatacoensis*. The columnar sections of Guerrero (in press), however, are likely to show that the Duke locality 28 is stratigraphically about 450 meters below the type locality of *S. tatacoensis*. Guerrero (in press) also obtained several radioisotopic dates from some horizons above the type horizon: 13.69±0.15, 13.59±0.17, 13.77±0.05, and 13.78±0.08 Ma, suggesting the middle Miocene age, about 13 to 14 Ma, for *S. victoriae*.

At Duke locality 21, a distal humerus (IGM 183420) and proximal humerus (IGM 182858) were collected, and both are allocated to *Cebupithecia sarmientoi* (Meldrum *et al.*, 1990; Meldrum, 1993; Meldrum and Kay, in press). The horizon of these specimens are about 400 meters lower than that of the type specimen (Fig. 2).

Cerro Gordo: Cerro Gordo, which means a large hill in Spanish, is located about 5 km southeast of La Victoria village, a few km east from the jeep road between Villavieja and La Victoria. In this area

the strata, which correspond to the La Victoria Formation of Guerrero (in press), generally dip very gently towards the west, striking almost NS, whereas at the west side of Cerro Gordo mountain the dip of the strata become very steep (50-60°) probably as the result of the east-west compression. This structure, which can be interpreted as a series of the echelon folds, continues from the northeast of Cerro Gordo mountain through the eastern part of El Dinde. Aerial photographs of this area clearly show this structure.

Another specimen of *Cebupithecia*, a partial pelvis and pelvic limbs (IGM 184667), were recovered at Duke locality 79, a few kilometers southeast of Cerro Gordo mountain in 1988 (Meldrum and Kay, 1990). The horizon of this specimen is almost same as the Duke locality 21, just below the Chunchullo Sandstone Beds (Fig. 2).

The holotype of *Lagonimico conclucatus*, a crushed, but beautifully preserved skull, was recovered at Duke locality 90 in 1988 (Kay, 1994). The locality is situated 3 km south of La Victoria village, east of the jeep road between Villavieja and La Victoria, corresponding to between the Tatacoa Sandstone Beds and the Chunchullo Sandstone Beds, about 230 meters below the base of the Molina Member (= "Monkey Unit" of Fields, 1959).

La Venta region

La Venta region represents the southern side of Q. Tatacoa, and is subdivided into three areas: El Dinde, Los Mangos, and El Cusco (Fig. 1). El Dinde and Los Mangos areas are divided by Q. Cervetana, and Los Mangos and El Cusco areas are divided by Q. La Venta. The sediments of La Venta region correspond to the upper part of the La Victoria Formation and the Villavieja Formation.

El Dinde: The strata of El Dinde area correspond to the lower part of the Molina Member (Takai *et al.* 1992) and the upper part of the La Victoria Formation (Guerrero, in press). Many primate fossils have been recovered there. The holotype (UCMP 38989) of *Stirtonia tatacoensis* was collected at the UC locality V4534 (Stirton, 1951). Stirton (1951) originally described the locality is located "about 180 meters east of Quebrada Tatacoa", but later Fields (1959) indicated that this locality, V4534, is situated west side of Q. Tatacoa and corresponds to the upper part of the "Cerbatana Gravels and Clays", but. If Stirton's description is right, the type locality of *S. tatacoensis* would be much lower than the Fields' allocation. Judging from the description of the type locality (Stirton, 1951), the west side of Q. Tatacoa is likely more probable than the east side.

An almost complete mandible of *Mohanamico hershkovitzi* (IGM 181500) was collected from the Duke locality 22 in 1980 (Luchterhand *et al.*, 1986). The locality stratigraphically corresponds to the lowest part of the Molina Member, Villavieja Formation (Takai *et al.*, 1992). A left mandible and left maxillary fragment of *Aotus dindensis* (IGM-KU 8601) were collected in 1986 from the Kyoto locality 9-86A, also corresponding to the lowest part of the Molina Member (Setoguchi and Rosenberger, 1987). These two localities are situated very near each other, and correspond to the almost same horizon. However, the taxonomic confusion among *Mohanamico* and *A. dindensis* is still far from the settlement (e. g. Kay, 1990; Rosenberger *et al.*, 1990). A right talus (IGM-KU 8802), referred to *A. dindensis*, was also collected at the same location as IGM-KU 8601 in 1988

(Gebo *et al.*, 1990). During 1986 field season a left maxillary fragment with C-P^2 of *Cebupithecia sarmientoi* (IGM-KU 8602) was also collected at the Kyoto locality 9-86B, corresponding to the same horizon as the *A. dindensis* (Setoguchi *et al.*, 1988). So there are three or four fossil primates recovered at El Dinde to date.

Los Mangos: The sediments of Los Mangos area correspond to the Molina Member of Takai *et al.* (1992). This area is also called "La Venta" in a narrow sense. "La Venta" has been traditionally used as a vast area yielding a rich middle Miocene fauna in Colombia, so in this paper we use Los Mangos as the place-name. University California Expedition Teams called this area "Monkey Locality" and named its stratigraphic unit "Monkey Unit" because of the discovery of many primate fossils, such as the holotypes of *Neosaimiri fieldsi* (UCMP 39205, right and left mandibles) and *Cebupithecia sarmientoi* (UCMP 38762, partial skull and numerous skeletal fragments) from UC locality V4517 (Stirton, 1951; Fields, 1959). In addition, an isolated M_1 of *Stirtonia* (UCMP 39204) was recovered from the UC locality V4523 (Stirton, 1951).

At Los Mangos, about 30 years later, more than 40 isolated teeth were recovered from a very small spot, named Kyoto site, probably situated 1-2 km west of the UC locality V4517, by the surface collecting and screening/washing. Among those specimens some large-size teeth were described as *Stirtonia tatacoensis* and *Kondous laventicus* (Setoguchi *et al.*, 1981; Setoguchi, 1985), and small-size teeth as *Micodon kiotensis* (Setoguchi and Rosenberger, 1985). Other many isolated teeth have not been described yet. Duke University team also recovered a left distal humerus of *Neosaimiri* (IGM 183512) at the Duke locality 54 in 1986 (Meldrum *et al.*, 1990; Meldrum, 1993).

El Cusco: El Cusco is very famous for its desolate scenery, and many tourists visit there every year. Stratigraphically this area corresponds to the Los Mangos Red, Las Lajas, and Tatacoa Red Members.

During 1988 field season a nearly complete mandible with right and left C-M_2 (IGM-KU 88001) was recovered from the Kyoto locality Masato site, and described as the representative of a new genus and species, "*Laventiana annectens*" (Rosenberger *et al.*, 1991). This locality corresponds to the lower part of the Tatacoa Red Member (Takai *et al.*, 1992). During the following two field seasons, numerous isolated teeth and postcranial remains were recovered from the same locality, Masato site (Takai, 1994; Nakatsukasa *et al.*, in prep.). Those isolated teeth, including the type specimen of "*Laventiana*" are now identified as *Neosaimiri fieldsi* (Takai, 1994). A right talus (IGM-KU 88003) recovered from the Masato site during the same field season was described as "*Laventiana*" (Gebo *et al.*, 1990), and another postcranial fragment, a left distal tibia (IGM 250436), recovered by Duke University team at the same locality (= Duke locality 32) in 1989 was also referred to "*Laventiana* (= *Neoisaimiri*)" (Meldrum and Kay, in press).

Besides the Masato site, at El Cusco there are some fossil localities yielding several primate fossils. The Chepe site is located about 200 meters northeast of the Masato site, and stratigraphically slightly lower than the Masato site. This locality consists of the firmly concreted sandstone bed and corresponds to the uppermost part of the Las Lajas Member. Several small isolated teeth referable to *Neosaimiri fieldsi* have been recovered there (Takai *et al.*, in prep.). Another fossil locality, the Gentil

site, is located about 1.5 km east of the Masato site, and three fragmentary isolated teeth referable to *N. fieldsi* were collected in 1990. This site is likely the almost same horizon as the Masato site. Ford *et al.* (1991) also report a left primate talus recovered from the Duke locality 43.

Several radioisotopic dates have been obtained from the sediments of El Cusco. Takemura *et al.* (1992) reported a detailed columnar section of this area, Tatacoa Red Member, and obtained several radioisotopic ages by the fission-track method: 12.6±0.5, 13.6±0.7, and 13.6±0.5 Ma. Guerrero (in press) also obtained a radioisotopic age by the $^{40}Ar / ^{39}Ar$ method, 12.23±0.11 Ma. These two dates independently obtained by different workers suggest the probability of the middle Miocene age for the Villavieja Formation.

LIST OF PRIMATE FOSSIL MATERIALS

Stirtonia and *"Kondous"*

Despite the discovery of many specimens, the reconstruction of *Stirtonia* is far from the settlement, because neither cranial fragments nor postcranial remains have been recovered until now. There are two species, *S. tatacoensis* and *S. victoriae*, discovered in the Tatacoa Desert to date. The latter comes from the stratigraphically lower horizon than the former, and differs from the former in larger molar size, in having the better-developed stylar shelf/cusps, and in having three rooted P^{3-4}.

S. tatacoensis was originally described as a new species of *Homunculus* (Stirton, 1951) on the basis of the morphology of the type specimen (UCMP 38989) and referred specimens (UCMP 39204 and 39206), both of which are of lower dentition, and was renamed as a new genus, *Stirtonia*, by Hershkovitz (1970). A close relationship to living howler monkey, *Alouatta*, has already been pointed out at that time. Since 1979 many isolated teeth, including upper dentition, have been discovered from the Kyoto site mainly by screening and washing, and identified as *S. tatacoensis* (Setoguchi *et al.*, 1981). As in lower molar morphology, upper molars of *S. tatacoensis* is very similar to those of *Alouatta*, confirming the close relationship between them. Their dentition, especially upper molars, show the typical folivorous molar pattern, well-developed shearing crest.

Setoguchi (1985) considered two upper molars, recovered from the Kyoto site, as being another fossil taxa, *"Kondous laventicus"*, relating to the living spider monkey, *Ateles*. He differentiated *"Kondous"* from *Stirtonia* by the following characteristics: smaller molar size, narrow stylar region, lack of *Alouatta*-like buccal cingulum, generally low-relief cusp pattern, and the situation of the hypocone and posthypocrista (Setoguchi, 1985). However, many authors regard "*Kondous*" as a junior synonym of *S. tatacoensis* (e.g. Kay, 1987), because those characteristics regarded as the diagnosis of *"Kondous"* can be considered as a feature of M^3 in *Stirtonia*, and because the holotype and referred specimen of "*Kondous*", right "M^1" and "M^2", preserve united single root.

The holotype of *S. victoriae* was recovered at San Alfonso area in 1985 and 1986 by Duke university team (Kay *et al.*, 1987), and a new specimen was recovered by Kyoto University team in 1994 at the same location (Takai, in prep.). *S. victoriae* strongly resembles to *S. tatacoensis* in the well development of crests and stylar cusps in upper molars, and in overall morphology of upper and lower molars. *S. victoriae*, however, differs from *S. tatacoensis* in its larger size, in having better developed molar crests, and in having three-rooted rather than two-rooted P^3 and P^4 (Kay, et al.,

Table 1. Fossil specimens of *Stirtonia spp.* and "*Kondous*". UCMP = University of California, Museum of Paleontology, Berkeley, CA; IGM = INGEOMINAS; KU = Kyoto University; DU = Duke University; UC = University of California. R: right, L: lift.

Specimen	No.	Descriptive paper	Description	Area	Locality
Stirtonia tatacoensis					
UCMP	38989	Stirton (1951), Hershkovitz (1970)	mandible	El Dinde	UC locality V4534
UCMP	39204	Stirton (1951)	R. M_1 and L. I_1	Los Mangos	UC locality V4517
UCMP	39206	Stirton (1951)	L. M_1	Los Mangos	UC locality V4523
IGM-KU	III-1	Setoguchi *et al.* (1981)	maxilla with P^{2-4}, maxilla with M^1, and M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8101	undescribed	L. I^2?	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8102	undescribed	R. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8103	undescribed	L. P^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8104	undescribed	L. P^4	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8105	undescribed	L. P^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8106	undescribed	L. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8203	undescribed	R. M^3? (chemically damaged)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8204	undescribed	R. M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8205	undescribed	R. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8206	undescribed	R. P_3 or dP_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8207	undescribed	R. C_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8208	undescribed	L. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8209	undescribed	R. C_1 (chemically damaged)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8210	undescribed	L. dP_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8211	undescribed	L. C^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8212	undescribed	L. M^{1or2}	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8213	undescribed	L. I_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8214	undescribed	L. M^{1or2}	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8215	undescribed	R. M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8216	undescribed	L. M^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8217	undescribed	R. dP_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8218	undescribed	L. P_4?	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8219	undescribed	L. dP_3?	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8220	undescribed	L. dP^4?	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8221	undescribed	L. dP^4? (chemically damaged)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8222	undescribed	L. M^1? (chemically damaged)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8223	undescribed	L. M^2?	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8224	undescribed	L. M^3 (chemically damaged)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8225	undescribed	R. M^1?	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8226	undescribed	R. M^2?	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8227	undescribed	R. dP^4? (chemically damaged)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8228	undescribed	R. dP^4? (chemically damaged)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8229	undescribed	R. P^2? (badly worn)	Los Mangos	Kyoto locality Kyoto site
Kondous laventicus					
IGM-KU	8201	Setoguchi (1985)	R. M^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	8202	Setoguchi (1885)	R. M^2	Los Mangos	Kyoto locality Kyoto site
Stirtonia victoriae					
IGM-DU	85-400	Kay *et al.* (1987)	maxilla with dP^{2-4} and M^{1-2}	San Alfonso	Duke locality 28
IGM-DU	86-534	Kay *et al.* (1987)	maxilla with dC-dP^4 and M^2	San Alfonso	Duke locality 28
IGM-KU	94001	undescribed	R. P_2 and P_3	San Alfonso	Duke locality 28

1987). These differences in size and morphology between them may indicate an interspecific variation among contemporaneous two species or an evolutionary transformation from stratigraphically older *S. victoriae* to younger *S. tatacoensis*. There is another possibility that those two species represent the sexual dimorphism, larger male (*S. victoriae*) and smaller female (*S. tatacoensis*), but it seems improbable unless both species will be collected together from the same location. A very large-size, robust upper canine of *S. tatacoensis* (IGM-KU 8211) and a large P_2 / P_3 ratio in *S. victoriae* (IGM-KU 94001) suggest the presence of the strong sexual dimorphism and a polygynous social organization in *Stirtonia*, just like in most living howler monkeys.

Micodon kiotensis

During 1984 field season a very small-size isolated primate M^1 was recovered from the soil at the Kyoto site by screening and washing. It was described as a first fossil marmoset, *Micodon kiotensis*. Other two isolated teeth, I^1 and P_4, were also referred to callitrichines because of their absolutely small size (Setoguchi and Rosenberger, 1985).

Though Setoguchi and Rosenberger (1985) regarded *Micodon* as an ancestor of callitrichines, Kay and Meldrum (in press) claim that *Micodon* should be treated as a junior synonym of *Neosaimir*. They regard the significant size difference between *Micodon* and *Neosaimiri* is attributable to the chemical erosion of the type specimen of *Micodon*. However, the discrepancies between *Micodon* and *Neosaimiri* in size and morphology are unlikely to be explained as an intraspecific variation or chemical transformation.

Mohanamico hershkovitzi and *Aotus dindensis*

Mohanamico hershkovitzi and *Aotus dindensis* are still point of contention. The holotype of *Mohanamico* was collected at El Dinde area in 1980, and that of *Aotus dindensis* was also discovered at the same area in 1986. The former is a nearly complete, slightly damaged at the symphysial region, mandible with right P_2-M_2 and roots of I_1-C, and with left I_2-C and P_3-M_2 (Luchterhand *et al.*, 1986). The latter is a left hemimandible with right I_1-left M_3 and a left maxillary fragment with roots of P^3-M^2 and the lingual half of M^3 (Setoguchi and Rosenberger, 1987).

Luchterhand *et al.* (1986) regarded *Mohanamico* as being probably allied to extant pitheciines by the following reasons: an elongate lateral incisor crown, a sharp canine crest running lingually from the protoconid, a relatively large and projecting P_2, a small metaconid, M_1-M_2 cristid obliqua reaching the apex of the protoconid, and loss of the hypoconid and hypoconid/entoconid sulcus. They also recognized that *Mohanamico* lacks several pitheciine-like characters such as posteriorly deepened mandible, rather posteriorly positioned I_2 with lateral compression, a massive P_2, mesiodistally elongated P_4, less pronounced molar crest, and crenulate enamel surface (Luchterhand *et al.*, 1986).

On the other hand, Setoguchi and Rosenberger (1987) regarded *A. dindensis* as being a middle Miocene species of the extant genus of night monkey, *Aotus*, on the basis of the following morphology: recumbent crowns of lower incisors, buccolingually compressed P_2, prow-like preprotocristid on $P_{2,3}$, not transversely broadened $P_{3,4}$, tall trigonid and faintly differentiated talonid cusps on $M_{1,2}$, and the presence of the curve of Spee on the mandibular corpus.

Table 2. Fossil specimens of *Micodon, Mohanamico, A. dindensis,* and *Cebupithecia* See Table 1 for abbriviations.

Micodon kiotensis

Specimen No.	Descriptive paper	Description	Area	Locality
IGM-KU 8401	Setoguchi and Rosenberger (1985)	L. M^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 8402	Setoguchi and Rosenberger (1985)	R. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 8403	Setoguchi and Rosenberger (1985)	L P_4	Los Mangos	Kyoto locality Kyoto site

Mohanamico hershkovitzi

Specimen No.	Descriptive paper	Description	Area	Locality
IGM 181500	Luchterhand *et al.* (1986)	mandible	El Dinde	Duke locality 22

Aotus dindensis

IGM-KU 86001	Setoguchi and Rosenberger (1987)	L mandible and L maxillae	El Dinde	Kyoto locality 9-86A
IGM-KU 8802	Gebo *et al.* (1990)	R. talus	El Dinde	Kyoto locality 9-86A

Cebupithecia sarmientoi

Specimen No.	Descriptive paper	Description	Area	Locality
UCMP 38762	Stirton (1949)	maxillae, mandible, and partial skeleton	Los Mangos	UC locality V4517
IGM-KU 8602	Setoguchi *et al.* (1988)	R. maxilla with C and P^2	El Dinde	Kyoto locality 9-86B
IGM 184667	Meldrumand Kay (1990)	partial pelvis	Cerro Gordo	Duke locality 79
IGM 183420	Meldrum and Kay (1990)	L distal humerus	San Alfonso	Duke locality 21
IGM 182858	Meldrum *et al.* (1990)	L proximal humerus	San Alfonso	Duke locality 21

These two fossil taxa, which were recovered and described independently at the almost same location, caused an intense controversy about their classification. Kay (1990) concluded that *A. dindensis* is a junior synonym of *Mohanamico* because (1) both species were collected from the same horizon, probably nearly same locality, (2) in size and proportions they are very similar to each other, and (3) in premolar and molar morphology there is no distinctive differences between them. Despite their emphasizing pitheciine-like features of *Mohanamico*, lack of other pitheciine-like characters is unlikely to support their conclusion. In contrast, Rosenberger *et al.* (1990) differentiate *A. dindensis* and *Mohanamico* by many detailed dental morphology, but they seem to particularize too minute characters of lower dentition, neglecting a possibility of the individual variations. A detailed direct comparison between these two type specimens would solve this serious problem, though, in our opinion, those two taxa should be conspecific and related to extant *Aotus*.

A right talus (IGM-KU 8802) recovered at El Dinde area in 1988 were referred to *A. dindensis*, because it is too small for *Stirtonia* and too large for *Micodon* in size, and is not similar to the talus of *Cebupithecia* or *Neosaimiri* (Gebo *et al.*, 1990). It closely resembles the talus of extant *Aotus* and *Callicebus*, suggesting an attribution to *Aotus dindensis* (or *Mohanamico hershkovitzi*).

Cebupithecia sarmientoi

The type specimen of *Cebupithecia sarmientoi* (UCMP 38762), which was discovered at Los Mangos area in 1945, is nearly 70 % of the whole skeletal elements. Not only dental elements but also postcranial remains of *Cebupithecia* resemble to those of extant *Pithecia*, suggesting a close relationship between them. *Cebupithecia* is surely specialized middle Miocene pitheciine, making the

position of *Mohanamico* as the "middle Miocene pitheciine" doubtful.

The several new specimens of *Cebupithecia* have been discovered during this decade. A maxillary fragment with C^1 and P^2 was collected at El Dinde area in 1986 (Setoguchi *et al.*, 1988). The horizon of this specimen corresponds to the almost same as the type specimen. On the other hand, a partial pelvis and hindlimbs and distal and proximal humeri were recovered at Cerro Gordo and San Alfonso areas, respectively (Meldrum *et al.*, 1990; Meldrum and Kay, 1990; Meldrum, 1993). These two specimens were discovered from the horizon about 400 m below the type horizon. Despite the large stratigraphic differences between the holotype and the referred specimens, they are allied to the same species, *C. sarmientoi*.

Unfortunately, dental remains, which is the most impotant fossil material for the taxonomic identification, have not yet been recovered in La Victoria region. Strictly speaking, therefore, the stratigraphical distribution of *Cebupithecia* is still problematic. A newly recovered pitheciine form makes this problem more difficult.

Neosaimiri fieldsi

The type specimen of *Neosaimiri* was discovered at Los Mangos area in 1945 (Stirton, 1951), and until recently the second specimens have not been discovered. During the 1988 field season, a relatively complete *Saimiri*-size mandible was collected at the Masato site of El Cusco area, and described as a representative of a new genus and species, *"Laventiana annectens"* (Rosenberger *et al.*, 1991). During 1989 and 1990 field seasons, numerous isolated teeth and postcranial fragments were collected at the same location as *"Laventiana"* mainly by washing and screening. Those materials contained not only lower dentition but also upper dentition and deciduous teeth. All these dental remains, including the type of "*Laventiana*", were carefully examined and conclusively classified into the same taxon, *Neosaimiri fieldsi*, which shows a remarkable intraspecific variation (Takai, 1994). However, some workers regards "*Laventiana*" as a second species, *N. annectens* partly because it comes from about 80 to 100 meters higher horizon than *N. fieldsi* (Kay, 1994; Kay and Meldrum, in press).

Neosaimiri is most similar to *Saimiri* among extant platyrrhines in the shape and size proportion of molar series and in the basic crown morphology. In addition, as in *Saimiri*, distinct sexual dimorphism is seen at least in upper and lower canines of *Neosaimiri*, suggesting a male-male competition. However, *Neosaimiri* is differentiated from *Saimiri* in the proportions of tooth series, with smaller incisors and larger molars; in the structure of the P^4 hypocone; and in the morphology of $M_{1\text{-}2}$, which shows strong polymorphism.

Numerous postcranial remains referred to *Neosaimiri* have been also discovered: a distal humerus (IGM 183512) at Los Mangos area; a right talus (IGM-KU 8803; Gebo *et al.*, 1990), a distal tibia (IGM 250436; Meldrum and Kay, 1993), and numerous remains from the Masato site. Nakatsukasa *et al.* (in prep.) show that, as in dental morphology, those postcranial remains most resemble *Saimiri* among extant platyrrhines in size and overall morphology, convincing a close relationship between *Saimiri* and *Neosaimiri*.

Several isolated teeth referred to *Neosaimiri* have been recovered at El Cusco area: Chepe site

Table 3. Fossil specimens of *Neosaimiri*. See Table 1 for abbrebiations.

Neosaimiri fieldsi

Specimen	No.	Descriptive paper	Description	Area	Locality
UCMP	39205	Stirton (1951)	R. and L. mandible	Los Mangos	UC locality V4517
IGM-KU	88001	Rosenberger *et al.* (1991)	mandible	El Cusco	Kyoto locality Masato site
IGM-KU	88003	Gebo *et al.* (1990)	R. talus	El Dinde	Kyoto locality Masato site
IGM	183512	Meldrum *et al.* (1990)	L. distal humerus	Los Mangos	Duke locality 54
IGM	250436	Meldrum and Kay (in press)	L. distal tibia	El Cusco	Duke locality 32 (= Masato site)
IGM-KU	89001	Takai (1994)	R. mandible with P_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89002	Takai (1994)	R. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89003	Takai (1994)	L. mandible with root of M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89004	Takai (1994)	L. I^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89005	Takai (1994)	L. P_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89006	Takai (1994)	L. mandible with M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89007	Takai (1994)	L. M_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89008	Takai (1994)	R. M^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89009	Takai (1994)	R. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89010	Takai (1994)	L. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89011	Takai (1994)	R. M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89012	Takai (1994)	L. M^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89013	Takai (1994)	R. P^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89014	Takai (1994)	L. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89015	Takai (1994)	L. P^4? (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89016	Takai (1994)	L. P^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89017	Takai (1994)	R. C^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89018	Takai (1994)	R. M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89019	Takai (1994)	R. M1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89020	Takai (1994)	R. dC_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89021	Takai (1994)	R. C_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89022	Takai (1994)	R. dP_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89023	Takai (1994)	L. P_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89025	Takai (1994)	R. mandible with P_{3-4}	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89027	Takai (1994)	L. P_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89028	Takai (1994)	L. P_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89029	Takai (1994)	L. mandible with P_4-M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89030	undescribed	L. talus	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89031	undescribed	L. talus	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89032	Takai (1994)	R. M_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89033	Takai (1994)	R. M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89034	Takai (1994)	R. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89035	Takai (1994)	L. dP^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89036	Takai (1994)	L. M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89037	Takai (1994)	R. dP^4? (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89039	Takai (1994)	L. M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89040	Takai (1994)	R. P^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89041	Takai (1994)	R. dP_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89042	Takai (1994)	L. P_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89043	Takai (1994)	L. dC^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89044	Takai (1994)	R. dP_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89045	Takai (1994)	L. P_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89046	Takai (1994)	R. dP^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU	89047	Takai (1994)	R. P^4	Los Mangos	Kyoto locality Kyoto site

Table 3 *Continued*

Specimen No.	Descriptive paper	Description	Area	Locality
IGM-KU 89048	Takai (1994)	R. dC^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89049	Takai (1994)	L. M^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89050	Takai (1994)	R. dP_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89051	Takai (1994)	R. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89052	Takai (1994)	L. M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89053	Takai (1994)	R. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89054	Takai (1994)	L. M^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89055	Takai (1994)	R. P^3? (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89056	Takai (1994)	R. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89057	Takai (1994)	R. dP^4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89058	Takai (1994)	R. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89059	Takai (1994)	R. P_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89060	Takai (1994)	R. dP_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89061	Takai (1994)	R. dP_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89063	Takai (1994)	L. I_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89064	Takai (1994)	L. dP_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89065	Takai (1994)	R. dC^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89066	Takai (1994)	L. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89068	Takai (1994)	R. I^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89070	Takai (1994)	R. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89071	Takai (1994)	R. P^4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89072	Takai (1994)	L. M^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89073	Takai (1994)	L. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89074	Takai (1994)	L. I^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89075	Takai (1994)	R. I^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89076	Takai (1994)	L. dP^4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89077	Takai (1994)	L. C^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89078	Takai (1994)	L. P^4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89079	Takai (1994)	L. P_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89080	Takai (1994)	L. M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89081	Takai (1994)	L. I_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89082	Takai (1994)	R. dP_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89084	Takai (1994)	L. dP_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89085	Takai (1994)	L. C_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89086	Takai (1994)	R. I_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89088	Takai (1994)	R. P_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89090	Takai (1994)	L. M_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89091	Takai (1994)	R. M^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89092	Takai (1994)	R. I_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89093	Takai (1994)	L. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89094	Takai (1994)	L. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89095	Takai (1994)	L. P_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89096	Takai (1994)	L. dC_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89097	Takai (1994)	R. dP^4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89098	Takai (1994)	L. dP_4 (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89101	Takai (1994)	R. dP^3 (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89102	Takai (1994)	L. dP^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89103	Takai (1994)	R. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89104	Takai (1994)	R. M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89105	Takai (1994)	R. P_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89106	Takai (1994)	R. P_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89108	Takai (1994)	L. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89110	Takai (1994)	R. M^{1or2}? (fragment)	Los Mangos	Kyoto locality Kyoto site

Table 3 *Continued*

Specimen No.	Descriptive paper	Description	Area	Locality
IGM-KU 89111	Takai (1994)	R. dP_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89112	Takai (1994)	R. I^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89114	Takai (1994)	R. C^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89115	Takai (1994)	R. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89116	Takai (1994)	L. dC_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89117	Takai (1994)	L. M_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89118	Takai (1994)	R. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89120	Takai (1994)	L. dC^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89121	Takai (1994)	L. mandible with M_{1-2}	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89122	Takai (1994)	L. P_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89123	Takai (1994)	Mandible with roots of R. I_{1-2} and L. I_1-C	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89124	Takai (1994)	L. P_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89125	Takai (1994)	R. dP_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89127	Takai (1994)	L. P^4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89128	Takai (1994)	R. dP^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89129	Takai (1994)	R. I_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89130	Takai (1994)	R. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89131	Takai (1994)	R. M^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89132	Takai (1994)	R. P_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89133	Takai (1994)	R. I_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89134	Takai (1994)	R. mandible with P_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89135	Takai (1994)	R. P_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89136	Takai (1994)	R. dC^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89137	Takai (1994)	L. I_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89138	Takai (1994)	R. I_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89139	Takai (1994)	R. mandible with M_2 and root of M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89140	Takai (1994)	R. maxilla with dP^{3-4}, M^1, and root of dP^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89142	Takai (1994)	R. maxilla with I^2 and root of I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89143	Takai (1994)	R. dC^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89144	Takai (1994)	L. C_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89145	Takai (1994)	R. M_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89146	Takai (1994)	L. dP^4? (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89147	Takai (1994)	L. P_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89150	Takai (1994)	R. M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89151	Takai (1994)	R. dP_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89152	Takai (1994)	L. M_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89153	Takai (1994)	L. dC_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89154	Takai (1994)	R. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89155	Takai (1994)	L. I^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89156	Takai (1994)	R. I_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89157	Takai (1994)	L. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89160	Takai (1994)	R. P^4? (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89171	undescribed	L. humeral head and surgical neck	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89172	undescribed	R. humeral head and surgical neck	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89173	undescribed	L. humeral head	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89174	undescribed	L. lateral half of humeral head	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89175	undescribed	L. proximal ulna	Los Mangos	Kyoto locality Kyoto site

Table 3 *Continued*

Specimen No.	Descriptive paper	Description	Area	Locality
IGM-KU 89176	undescribed	L. olecranon	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89177	undescribed	R. proximal ulnar shaft	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89178	undescribed	R. olecranon	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89179	undescribed	L. distal ulna	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89180	undescribed	R. distal radius	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89181	undescribed	L. femoral head and neck	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89182	undescribed	R. femoral head	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89183	undescribed	L. femoral head	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89184	undescribed	L. femoral head	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89185	undescribed	L. femoral head	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89186	undescribed	R. proximal femoral shaft	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89187	undescribed	L. distal femur	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89188	undescribed	R. distal femur	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89189	undescribed	L. distal femur (deformed)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89190	undescribed	L. medial condyle	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89192	undescribed	L. proximal tibia	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89194	undescribed	L. distal tibia	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89195	undescribed	R. distal tibia	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89196	undescribed	R. distal fibula	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89197	undescribed	R. distal fibula	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89199	undescribed	R. talus	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89200	undescribed	R. talar body	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89201	undescribed	L. calcaneus	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89202	undescribed	L. calcaneus	Los Mangos	Kyoto locality Kyoto site
IGM-KU 89203	undescribed	L. calcaneus	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90001	Takai (1994)	R. M^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90002	Takai (1994)	R. M^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90003	Takai (1994)	R. M1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90004	Takai (1994)	R. M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90005	Takai (1994)	L. maxilla with dP^{2-4} and M^{1-2}	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90006	Takai (1994)	R. M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90007	Takai (1994)	R. P^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90008	Takai (1994)	R. P^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90009	Takai (1994)	R. P^4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90010	Takai (1994)	R. M^{1or2}? (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90011	Takai (1994)	L. P^3? (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90013	Takai (1994)	R. M^{1or2}? (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90015	Takai (1994)	R. P_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90016	Takai (1994)	R. P_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90017	Takai (1994)	L. dP_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90018	Takai (1994)	L. dP_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90019	Takai (1994)	R. M_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90020	Takai (1994)	R. M_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90022	Takai (1994)	L. C^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90023	Takai (1994)	L. C_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90024	Takai (1994)	L. I_2 (fragment)	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90025	Takai (1994)	L. I^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90026	Takai (1994)	L. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90027	Takai (1994)	L. maxilla with C^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90028	Takai (1994)	L. maxilla with P^4-M^1 and roots of P^3 and M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90029	Takai (1994)	L. M^2	Los Mangos	Kyoto locality Kyoto site

Table 3 *Continued*

Specimen No.	Descriptive paper	Description	Area	Locality
IGM-KU 90030	Takai (1994)	L. M^2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90031	Takai (1994)	L. I^1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90032	Takai (1994)	L. P^3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90033	Takai (1994)	R. C_1	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90034	Takai (1994)	L. dP_3	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90035	Takai (1994)	L. dP_4	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90036	Takai (1994)	Mandible fragments with R. dP_4, $M_{1\text{-}2}$, L. dP_4, $M_{1\text{-}2}$, and unerupted P_2	Los Mangos	Kyoto locality Kyoto site
IGM-KU 90041	undescribed	R. M_3	Los Mangos	Kyoto locality Gentil site
IGM-KU 90042	undescribed	L. M_3? (fragment)	Los Mangos	Kyoto locality Gentil site
IGM-KU 90043	undescribed	L. C_1?	Los Mangos	Kyoto locality Chepe site
IGM-KU 90044	undescribed	L. I^1?	Los Mangos	Kyoto locality Chepe site
IGM-KU 90045	undescribed	L. dP^4	Los Mangos	Kyoto locality Chepe site
IGM-KU 90046	undescribed	R. M_3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90047	undescribed	R. M3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90048	undescribed	R. P_{3or4}	Los Mangos	Kyoto locality Chepe site
IGM-KU 90049	undescribed	R. M_{1or2}	Los Mangos	Kyoto locality Chepe site
IGM-KU 90050	undescribed	R. M_1	Los Mangos	Kyoto locality Chepe site
IGM-KU 90051	undescribed	L. dP^3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90052	undescribed	R. I_2	Los Mangos	Kyoto locality Chepe site
IGM-KU 90053	undescribed	R. dP^3? (fragment)	Los Mangos	Kyoto locality Chepe site
IGM-KU 90054	undescribed	L. P_2	Los Mangos	Kyoto locality Chepe site
IGM-KU 90055	undescribed	L. P^2	Los Mangos	Kyoto locality Chepe site
IGM-KU 90056	undescribed	R. M_3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90057	undescribed	R. dP^2	Los Mangos	Kyoto locality Chepe site
IGM-KU 90058	undescribed	R. dP^3? (fragment)	Los Mangos	Kyoto locality Chepe site
IGM-KU 90059	undescribed	L. M_3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90060	undescribed	L. M_3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90061	undescribed	L. P^3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90062	undescribed	R. P^4? (fragment)	Los Mangos	Kyoto locality Chepe site
IGM-KU 90063	undescribed	L. C_1	Los Mangos	Kyoto locality Chepe site
IGM-KU 90067	undescribed	R. M_3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90070	undescribed	R. M_1	Los Mangos	Kyoto locality Chepe site
IGM-KU 90071	undescribed	R. P_4	Los Mangos	Kyoto locality Chepe site
IGM-KU 90073	undescribed	R. M_3	Los Mangos	Kyoto locality Chepe site
IGM-KU 90074	undescribed	L. dP^4	Los Mangos	Kyoto locality Chepe site
IGM-KU 93001	undescribed	L. C	Los Mangos	Kyoto locality Chepe site
IGM-KU 93002	undescribed	R. dP^3	Los Mangos	Kyoto locality Chepe site

Table 4. Fossil specimen of *Lagonimico* and other new forms. See Table 1 for abbrebiations.

Lagonimico conclucatus

Specimen No.	Descriptive paper	Description	Area	Locality
IGM 184531	Kay (1994)	crushed skull	Cerro Gordo	Duke locality 90
undescribed callitrichine				
IGM 184332	Kay and Meldrum (in press)	R. mandible with dP_{2-4} and M_{1-3}, and unerupted P_{3-4}	Cerro Gordo	Duke locality 40
undescribed pitheciine				
?		mandible	?	?
genus and species indet.				
IGM 184074	Ford *et al.* (1991)	L. talus	El Cusco	Duke locality 43

and Gentil site. Chepe site is stratigraphically slightly lower than the Masato site, and Gentil site is almost same horizon as the Masato site (Fig. 1). The presence of these new materials of *Neosaimiri* may suggest that it was widely distributed in the present during middle Miocene age.

Other new forms

Recently Duke University team recovered two new platyrrhine forms, a right mandible of the small-size callitrichine (Kay and Meldrum, in press) and a medium-size pitheciine mandible (Kay, personal communication). In the description of the former, they conclude that *Micodon* is a junior synonym of *N. fieldsi* and the new form is referable to Callitrichinae (Kay and Meldrum, in press). Judging from the molar size, however, it should be examined first whether the new callitrichine form belong to *Micodon* or not. However, an isolated P^4 allocated to *Micodon* is unlikely similar to that of the new form, so the classification of these taxa seems far from the settlement.

On the other hand, the larger new form shows an obvious pitheciine-like dental morphology, suggesting a relationship to extant pitheciines, but does not resemble the mandible of *Cebupithecia*. If the generic status of this new form as a new pitheciine taxon is established, there should be two pitheciine taxa during the middle Miocene age in Colombia.

FUTURE WORKS

At present it has not beeen demonstrated clearly that there is a apparent faunal transition between the mammalian fossil assemblages of the La Victoria and Villavieja Formations. As indicated in Figure 2, there are three main levels yielding primate fossils. The lower level corresponds to the horizon above and below the Chunchullo Sandstone Bed (Guerrero, in press), yielding *S. victoriæ*, *Cebupithecia*, *Lagonimico*, and new callitrichine. The middle level is the "Monkey Unit" of Fields (1959), which corresponds to the lower part of the Molina Member of Takai *et al.* (1992), yielding many fossil taxa have bee recovered: *Neosaimiri*, *Stirtonia* (including "*Kondous*"), *Cebupithecia*, *Micodon*, *A. dindensis*, and *Mohanamico*. Upper level is the lower part of the Tatacoa Red Member of Takai *et al.* (1992), yielding dozens of dental and postcranial fragments of *Neosaimiri*.

There is no fossil species which has been recovered from all the levels to date, but some taxa are collected from two levels: *Cebupithecia* comes from the lower and middle levels, *Neosaimiri* from

the middle and upper levels, and *Stirtonia* from the lower and middle levels. Though *Stirtonia* is classified into two species, stratigraphically older *S. victoriae* and younger *S. tatacoensis*, the allocation of other two genera, *Cebupithecia* and *Neosaimiri*, has not yet established. All specimens of *Cebupithecia* collected from the lower level are allocated to the same species, *C. sarmientoi*, on the basis of their resemblance in postcranials to the type specimen (Meldrum and Kay, 1990; Meldrum *et al.*, 1990; Meldrum, 1993). However, the dental remains, which is one of the most important clue to classify fossil specimens, have not yet collected from the lower level.

On the other hand, Kay (1994) and Kay and Meldrum (in press) admit two species in *Neosaimiri*, *N. fieldsi* and "*N. annectens*" mainly because of their stratigraphic positions, though the stratigraphic difference between lower and middle levels of *Cebupithecia* is much larger than that of *Neosaimiri* (Fig. 2). If it is admitted that there are two species in *Neosaimir*, it seems reasonable to classify *Cebupithecia* into two species on the basis of their stratigraphic positions. We are faced with a good example of the "transformation of species in time", that is, in other word, "phyletic evolution" or "phyletic speciation". Anyway, the total analysis of the La Venta vertebrate fauna will reveal the process of the faunal transition and the radiation of the "modern" platyrrhine taxa.

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